

Above- and Belowground Productivity and Soil Carbon Dynamics of Pasture Mixtures

R. Howard Skinner,* Matt A. Sanderson, Benjamin F. Tracy, and Curtis J. Dell

ABSTRACT

Increasing plant species diversity could enhance forage yield, resistance to weed invasion, and soil C accumulation in grazed pastures. Three forage mixtures (2, 3, or 11 species) were established on a farm in eastern Pennsylvania and grazed by dairy heifers or managed under a three-cut hay system from 1999 to 2002. Net canopy photosynthesis was measured from early April to early October 2000 to 2002. Root distribution to a depth of 60 cm was measured in mid-September each year, and soil C and N concentrations to a 15-cm depth were determined in May 1999 and September 2002. The 11-species mixture yielded 43% more forage dry matter than the two-species mixture. This difference was mainly due to the inclusion of a few highly productive forage species in the 11-species mixture. Canopy photosynthesis did not differ among mixtures in the spring, but in the summer was 50% greater in the 3- and 11-species mixtures than the two-species mixture. The 11-species mixture also had 30 to 62% greater root biomass than the other two mixtures and a greater proportion of roots in deeper soil layers. Soil C either remained unchanged or decreased, depending on species composition, with the greatest decrease occurring in the 11-species mixture. No relationship existed between changes in soil C concentration and either canopy photosynthesis or above- and belowground productivity. Deeper rooting could reduce drought stress by increasing access to deep soil moisture. Selecting forage mixtures to include specific desirable traits, such as greater rooting depth, could result in improved pasture performance.

REDUCED forage production of pastures during periods of summer drought presents a significant risk to producers who are constantly searching for ways to reduce that risk. Considerable ecological research suggests that greater diversity of species in grassland ecosystems increases and stabilizes productivity under stressful conditions (Tilman, 1999; Minns et al., 2001), although others suggest that there is no general benefit from increased plant diversity (Huston et al., 2000; Wardle et al., 2000). It is not clear, however, how these concepts relate to grazed pasture systems (Sanderson et al., 2004).

Benefits from increased species diversity are often greatest under harsh environmental conditions and have been associated with: (i) improved use of scarce resources (Spehn et al., 2000b); (ii) facilitation of the growth and survival of one or more species by a companion species (Bertness, 1998); or (iii) an increased probability of in-

cluding the most productive species for a given environment (Wardle, 1999). Besides improving grassland productivity, increased species richness can reduce the invasion of weedy species (Fargione et al., 2003; Zavaleta and Hulvey, 2004; Tracy and Sanderson, 2004).

Forage yield is a function of net photosynthetic inputs (photosynthesis minus respiration) and of the partitioning of those inputs between above- and belowground tissues. Root production during moisture stress can be particularly important because enhanced rooting depth can increase access to the greater soil moisture usually found deeper in the soil profile. Skinner et al. (2004) found that roots of complex, five-species mixtures were distributed deeper in the soil profile than roots of simple, two-species mixtures. Forage yield was also greater in the five-species mixtures under drought conditions. While many studies have looked at aboveground productivity of grasslands, much less information is available on canopy photosynthetic rates and on root production and distribution in the soil profile.

Soil organic carbon (SOC) generally increases following the conversion of cropland to pasture (Schnabel et al., 2001). Distribution of SOC within the soil profile is a function of plant functional types with shoot vs. root allocation and vertical root distribution affecting the distribution of SOC with depth (Jobbagy and Jackson, 2000). Thus, any change in biomass allocation patterns resulting from shifts from shallow- to deep-rooted species could significantly change whole-system soil C storage (Gill et al., 1999); however, it is not clear how changes in species or functional group richness might affect SOC. Wardle et al. (1999) found that soil C and N concentrations were insensitive to the removal of plant functional groups, possibly because they reflect longer term changes than could be detected during the 3-yr study. Although increased plant biodiversity can increase C inputs into the ecosystem, diversity effects on soil herbivore and decomposer communities can be highly variable and may or may not also accelerate soil C turnover and loss from the system (Naeem et al., 1999; Wardle et al., 1999; Spehn et al., 2000a; Wardle et al., 2004). The paucity of direct evidence for biodiversity effects on SOC accumulation along with mixed results from decomposer studies suggests that much remains to be learned about how changes in plant biodiversity affect SOC.

There are few studies that have examined how species in complex forage mixtures persist in intensively managed pastures. We conducted an on-farm study to determine the persistence and yield of complex mixtures of forage species compared with a simple grass-legume mixture, and to examine how photosynthetic inputs and root-shoot partitioning affect soil C sequestration. We

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Abbreviations: SOC, soil organic carbon.

hypothesized that canopy photosynthesis and shoot and root biomass would increase as mixture complexity increased, and that increased biomass production would lead to increased C accumulation in the soil profile.

MATERIALS AND METHODS

The study was conducted on a producer owned and operated farm in Berks County, eastern Pennsylvania (40°28'15" N, 76°10'19" W) that had previously been planted to winter wheat (*Triticum aestivum* L.). Soils on the farm are Weikert and Berks silt loams (loamy-skeletal, mixed, active, mesic Lithic Dystrudepts). These soils are well drained, contain a high amount (10–50%) of coarse rock fragments, and have low water-holding capacities. At the beginning of the study in 1997, soil pH was 6.4 and available P and K levels to a 15-cm depth averaged 88 and 142 kg ha⁻¹, respectively. The producer applied lime at 2240 kg ha⁻¹ in the spring of 2000.

Two 0.4-ha paddocks of 2- and 11-species mixtures were no-till planted with a Tye Pasture Pleaser drill (Tye Co., Lockney, TX) on 28 Aug. 1997. The two-species mixture included 'Pennlate' orchardgrass (*Dactylis glomerata* L.) and 'Will' white clover (*Trifolium repens* L.). The 11-species mixture included Pennlate orchardgrass, Will white clover, 'Puna' chicory (*Cichorium intybus* L.), 'Saratoga' smooth bromegrass (*Bromus inermis* Leyss.), 'Barcel' tall fescue (*Festuca arundinacea* Schreb.), 'Matua' prairie grass (*Bromus willdenowii* Kunth.), 'Paddock' meadow bromegrass (*Bromus bilbersteinii* Roem. & Schult.), 'Norcen' birdsfoot trefoil (*Lotus corniculatus* L.), 'Alfagraz' alfalfa (*Medicago sativa* L.), 'Climax' timothy (*Phleum pratense* L.), and 'Palaton' reed canarygrass (*Phalaris arundinacea* L.). Glyphosate [N-(phosphonomethyl) glycine] was applied to the wheat stubble at 1.12 kg a.i. ha⁻¹ 2 wk before planting. The two-species mixture was a common grass and legume combination frequently used in northeastern USA pastures. The 11-species mixture represented the range of species commonly found in humid-temperate pastures, and was chosen to maximize the number of species that might reasonably be included in a pasture mixture.

The producer selected the species and custom hired the planting of the three-species mixture, but the establishment procedures were essentially the same. The three-species mixture included Pennlate orchardgrass, Alfagraz alfalfa, and Puna chicory. We selected two 0.4-ha paddocks within this planting for monitoring. In May 1999, we installed one 6.1- by 6.1-m grazing enclosure in each treatment paddock. The area inside the enclosure was used to emulate a three-cut (late May, July, and August) hay management scenario. The area inside the enclosure was fertilized with 40 kg N ha⁻¹ in April of each year. An automated weather station at the site recorded rainfall, air temperature, and soil moisture at depths of 10 and 60 cm.

The paddocks were not grazed, but were cut twice for hay in 1998. Beginning in 1999 and continuing into 2002, paddocks were rotationally grazed by 45 to 60 Holstein dairy heifers for a 1- to 2-d period of stay on a 30- to 45-d rotation interval. The heifers grazed other paddocks on the farm when not grazing experimental plots. Grazing started in late April and ended the first week of October each year. All paddocks in the study were cut for hay once in late May or June each year of grazing. The producer discontinued grazing on the farm in late 2002.

Dry matter yield was measured from 1999 to 2002 by clipping forage from two quadrats (1 by 1 m) inside and outside of each enclosure to a 5-cm stubble height on three dates (June, July, and August) in each year. The aboveground biomass was hand sorted to species once in midsummer each year and the botanical composition was calculated. The

experimental design was a randomized complete block. The two pastures of each treatment were considered replicates. The MIXED procedure in SAS (SAS Institute, 1998) was used for statistical analysis.

Net canopy photosynthesis was measured at midday (1000–1400 h) on seven to eight dates (every 3–4 wk) from early April to early October in 2000, 2001, and 2002 using a LI-6400 open-path photosynthesis system (Li-Cor Inc., Lincoln, NE) combined with a 1-m³ flow-through canopy chamber (Long et al., 1996). Seasonal estimates of photosynthetic rates were obtained by grouping readings taken in April and May (spring), June through August (summer), and September and October (fall). In September of each year, root biomass and distribution were determined by taking four, 5-cm-diameter by 60-cm-deep soil cores from each pasture. Roots were washed free of soil, ashed at 540°C, and root dry weight expressed on an ash-free basis.

Soil samples for SOC determinations were collected to a depth of 15 cm in May 1999 and again in September 2002. Samples were divided into 0- to 5- and 5- to 15-cm segments, air dried, crushed, and passed through a 2-mm sieve to remove stones and large root fragments. Visible roots were removed and sieved soil was ground with a mortar and pestle. Approximately 30 mg of soil was combusted in an EA 1100 elemental analyzer (CE Elantech, Lakewood, NJ) to determine total C and N concentrations (Nelson and Sommers, 1996). Since soils were well drained and somewhat acidic, they were assumed to contain essentially no inorganic C (carbonates). Therefore, all measured soil C was considered to be organic. Although predominately organic, the total N measured also included any NH₄- or NO₃-N present.

RESULTS AND DISCUSSION

White clover, birdsfoot trefoil, reed canarygrass, and timothy did not establish well in the complex mixture and did not contribute significantly to sward dry matter. Hay management during 1998 and the practice of taking one cutting of hay during the grazing seasons of 1999 to 2002 probably affected the establishment and survival of white clover and birdsfoot trefoil. This management probably allowed the taller growing species to gain a competitive advantage by shading these low-growing species. Reed canarygrass is slow to establish and can be sensitive to seedling competition (Sheaffer and Marten, 1995), suggesting that it might not be appropriate for multiple-species mixtures. On the other hand, timothy is generally easy to establish but does not persist under droughty conditions such as occurred during this experiment (McElroy and Kunelius, 1995).

The pattern of change in botanical composition differed among mixtures, depending on whether they were managed for hay or grazing (Fig. 1). The two-species mixture under hay management was dominated by orchardgrass. Under grazing management, however, the grass/legume ratio fluctuated greatly. The three-species mixture, whether managed for hay or grazing, became dominated by orchardgrass by 2001; however, the percentage of orchardgrass decreased during 2002 and 2003, with a corresponding increase in alfalfa. Tall fescue became the dominant species in the 11-species mixture by 2001 under both hay and grazing management. The dominance of tall fescue continued to increase after 2001 when managed for hay. The proportion of tall fescue in

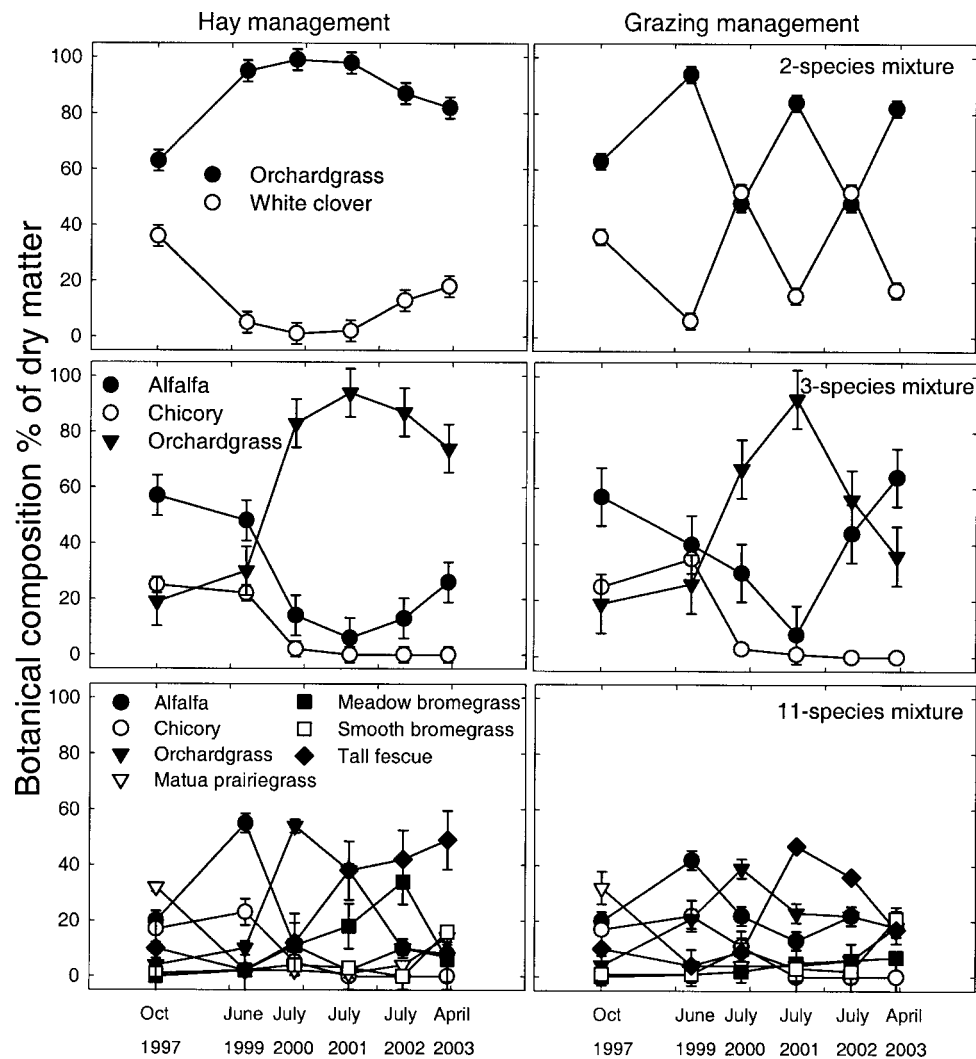


Fig. 1. Botanical composition of three forage mixtures under grazing or haying management in southeastern Pennsylvania. The mixtures were two species (orchardgrass and white clover), three species (orchardgrass, alfalfa, and chicory), and 11 species (alfalfa, orchardgrass, chicory, white clover, meadow bromegrass, smooth bromegrass, birdsfoot trefoil, Matua bromegrass, tall fescue, reed canarygrass, and timothy). White clover, reed canarygrass, timothy, and birdsfoot trefoil did not establish in the complex mixture. Grazing exclosures were installed in May 1999. Data are averages of two replicate pastures for each sampling date. Error bars within each management treatment represent pooled year \times mixture \times species standard errors.

the complex mixture decreased under grazing after 2001. By April 2003, tall fescue, alfalfa, smooth brome, Matua prairiegrass, and orchardgrass each comprised about 15 to 20% of the total biomass. Alfalfa became a small component of the 11-species mixture managed for hay, but maintained a relatively stable proportion of the sward under grazing. Chicory did not persist after 1999 in either the 3- or 11-species mixtures, whether managed for hay or grazing. Of the 11 species originally planted for the complex mixture in 1997, only six species persisted into the spring of 2003. Thus, in terms of planted species, the complex forage mixture tended to become less species rich with time whether cut for hay or grazed.

Nonplanted species, that is, weeds, comprised <3% of the aboveground biomass in all mixtures through the fall of 2001 (data not shown). In 2002, the percentage of weeds increased to about 8% in the two-species mixture but remained unchanged in the 3- and 11-species mixtures. Thus, weeds comprised a small and relatively in-

significant proportion of plant biomass throughout the experiment, although the least diverse mixture had the greatest proportion of weeds, as others have also observed (Naeem et al., 2000; Kennedy et al., 2002; Tracy and Sanderson, 2004).

There was no treatment \times year interaction for dry matter yield. When averaged across mixtures, yield under hay management was lower in 1999 than in the other 3 yr, which did not differ from each other (Table 1). Under grazing, yield was again lowest in 1999, but also reduced in 2001 compared with 2000 and 2002. When averaged across years, dry matter yield was greatest with the 11-species mixture under grazing, whereas yield was greatest with the 3- and 11-species mixtures under hay management (Table 1). The primary advantage of the 3- and 11-species mixtures compared with the two-species mixture was the inclusion of drought-tolerant species such as alfalfa in the three-species mixture and tall fescue and alfalfa in the 11-species mixture on this

Table 1. Dry matter yields of three forage mixtures under grazing or haying management in southeastern Pennsylvania. The mixtures were orchardgrass and white clover (two species); orchardgrass, alfalfa, and chicory (three species); and alfalfa, orchardgrass, chicory, white clover, meadow bromegrass, smooth bromegrass, birdsfoot trefoil, Matua bromegrass, tall fescue, reed canarygrass, and timothy (11 species). Data are averages of two replicate pastures and 4 yr.

Mixture and year	Haying management	Grazing management
Mixture	kg ha ⁻¹	
Two species	4508 b†	3563 b
Three species	5843 a	3236 b
11 species	6601 a	5150 a
Year		
1999	4118 b	2027 b
2000	6872 a	5233 a
2001	5725 a	3089 b
2002	5887 a	5585 a

† Means within a management treatment followed by the same letter are not significantly different at $P < 0.05$.

drought-prone soil. Chicory was included in the planting as another drought-tolerant species, but did not persist well enough to contribute to yield of either the 3- or 11-species mixture. By 2000, the three-species mixture under grazing had become essentially a two-species mixture of alfalfa and orchardgrass. The resulting yield increase compared with the two-species mixture probably resulted from replacing the drought-sensitive white clover in the two-species mixture with the more drought-tolerant alfalfa—an example of the “sampling effect” mechanism for explaining plant species diversity effects (Minns et al., 2001). The three-species mixture may not have produced as well under hay management compared with grazing because it had essentially become an orchardgrass monoculture (Fig. 1) and thus lacked the productivity during drought and N₂-fixation capacity provided by alfalfa.

When compared across the entire grazing season, neither mixture complexity ($P = 0.37$) nor harvest strategy (grazed vs. cut; $P = 0.43$) had a significant effect on overall midday photosynthetic rates, although a trend existed for photosynthesis to increase with increasing number of species in the mixture (6.8, 7.2, and 7.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for the 2-, 3-, and 11-species mixtures, respectively). Differences among mixtures were observed during the summer when photosynthesis in the 3- and 11-species mixtures was 50% greater than in the two-species mixture (Table 2). A significant year \times season interaction for photosynthetic rate was also found (Table 3). Photosynthetic rate was always greatest in the spring. Fall photosynthetic rates were greater than

Table 2. Seasonal differences in midday canopy photosynthetic rates for pastures in eastern Pennsylvania differing in species complexity. Values ± 1 SE are averaged across harvest strategy (cut vs. grazed) and year (2000–2002).

Mixture	Net photosynthesis		
	Spring	Summer	Fall
	$\mu\text{mol m}^{-2} \text{s}^{-1}$		
Two species	11.0 \pm 1.0	3.7 \pm 0.7	5.5 \pm 0.7
Three species	10.5 \pm 0.9	5.7 \pm 1.1	4.9 \pm 0.7
11 species	11.2 \pm 0.9	5.6 \pm 0.9	6.7 \pm 1.0

Table 3. Year \times season effects on midday canopy photosynthetic rates. Values ± 1 SE are averaged across harvest strategy (cut vs. grazed) and mixture complexity (2, 3, and 11 species).

Year	Net photosynthesis		
	Spring	Summer	Fall
	$\mu\text{mol m}^{-2} \text{s}^{-1}$		
2000	12.7 \pm 1.2	4.9 \pm 0.7	6.7 \pm 0.7
2001	9.4 \pm 0.7	6.4 \pm 1.0	4.0 \pm 0.8
2002	10.0 \pm 0.9	3.6 \pm 0.8	6.0 \pm 1.1
Mean	10.9 \pm 0.6	5.0 \pm 0.5	5.7 \pm 0.5

summer rates in 2000 and 2002, but rates during the summer were greater than in the fall in 2001. The greatest spring and fall photosynthetic rates occurred in 2000, with the lowest rates in 2001. In contrast, the greatest summer photosynthetic rate occurred in 2001, which was relatively cool and wet during July, and the lowest in 2002, when severe drought developed.

The 11-species mixture had greater total root biomass and greater biomass in the 5- to 15-, 15- to 30-, and 30- to 60-cm depths than the other two mixtures ($P < 0.05$). Root distribution extended deeper into the soil profile as mixture complexity increased (Table 4). In the two-species mixture, 73% of root biomass was found in the top 5 cm of the soil profile compared with 59% in the three-species mixture and 48% in the 11-species mixture. At the same time, the 30- to 60-cm layer contained 4, 8, and 12% of total root biomass in the 2-, 3-, and 11-species mixtures, respectively. The 3- and 11-species mixtures originally contained the deep-rooted species alfalfa and chicory; however, chicory disappeared from the mixtures before root data were collected and alfalfa generally averaged <20% of aboveground biomass in the 11-species mixture during the 2000 to 2002 growing seasons (Fig. 1). The deeper rooting profile with increased species diversity appeared to be related as much to a redistribution of grass roots within the soil profile as it was to inclusion of the deep-rooted species. Wardle and Peltzer (2003) showed that interspecific interactions can increase the ratio of deep to shallow roots. They suggested that the change in ratio between deep and shallow roots may have resulted from competition reducing growth in the upper layers while promoting growth at greater depths. Although we were not able to detect a significant difference among treatments in the 0- to 5-cm layer because of high variability within treatments

Table 4. Root biomass distribution to a depth of 60 cm for forage mixtures of increasing species complexity. Data are averaged across harvest strategy (cut vs. grazed) and year (2000–2002). Values ± 1 SE.

Depth	Ash-free dry weight		
	Two species	Three species	11 species
	kg ha ⁻¹		
0–5 cm	1860 \pm 284 (73†)	1200 \pm 223 (59)	1580 \pm 249 (48)
5–15 cm	380 \pm 28 (15)	450 \pm 62 (22)	810 \pm 118 (25)
15–30 cm	200 \pm 23 (8)	230 \pm 27 (11)	510 \pm 77 (16)
30–60 cm	90 \pm 13 (4)	150 \pm 29 (8)	410 \pm 51 (12)
Total	2540 \pm 294	2030 \pm 277	3300 \pm 285

† Values in parentheses indicate the percentage of total root biomass found in that particular soil layer. Total may not sum to 100% because of rounding error.

Table 5. Effect of species complexity on changes in soil C and N concentrations and C/N ratio after being grazed for four growing seasons. Samples were collected in May 1999 and September 2002. Data are ± 1 SE.

Mixture	Nitrogen		Carbon	
	1999	2002	1999	2002
	g kg ⁻¹			
	0- to 5-cm depth			
Two species	2.1 \pm 0.1	2.2 \pm 0.1	19.6 \pm 2.0	19.1 \pm 0.9
Three species	1.6 \pm 0.2	1.7 \pm 0.1	14.3 \pm 1.7	16.6 \pm 0.9
11 species	2.0 \pm 0.2	1.9 \pm 0.1	19.6 \pm 2.1	15.6 \pm 1.0
	5- to 15-cm depth			
Two species	1.5 \pm 0.1	1.5 \pm 0.1	12.4 \pm 0.5	10.5 \pm 0.2
Three species	1.2 \pm 0.1	1.2 \pm 0.1	10.6 \pm 0.9	10.4 \pm 0.5
11 species	1.3 \pm 0.1	1.3 \pm 0.1	10.8 \pm 0.5	8.8 \pm 0.3

(Table 4), the two-species mixture appeared to have greater root biomass in that layer, which would support the hypothesis of Wardle and Peltzer (2003). Harvest strategy had no effect on total root biomass ($P = 0.59$) or on distribution within the soil profile. The top 5 cm contained 60% of total root biomass when plots were cut for hay, compared with 58% under grazing.

Total soil N concentration remained constant during the course of the experiment for all mixtures and at both depths ($P > 0.97$). Changes in SOC concentration varied depending on mixture and soil depth (Table 5). At the 0- to 5-cm depth, SOC concentration decreased from 1999 to 2002 in the 11-species mixture ($P < 0.05$), but remained unchanged in the two- and three-species mixtures. At the 5- to 15-cm depth, SOC decreased in the 2- and 11-species mixtures ($P < 0.05$) and again was unchanged in the three-species mixture. Within a given soil depth, there was no relationship between changes in SOC and root biomass of the respective mixtures. There was also no relationship between changes in soil C and net photosynthetic rates. When the 0- to 5- and 5- to 15-cm layers were combined, however, the 11-species mixture had the greatest root biomass but also lost the most SOC, while the three-species mixture had the least root biomass yet was the only mixture not to show a decrease in SOC.

Contrary to our results, conversion from row crops to pasture is usually expected to cause an increase in SOC (Follett et al., 2001), and it is possible that, over time, these pastures would have accumulated C as well. This

study occurred during a particularly dry period (Table 6), however, with rainfall averaging only 84% of normal during the 42-mo duration of the experiment. July and August for all years were especially dry, averaging 51% of normal. In all, 33 of the 42 mo in the study had lower than average precipitation. Continuous eddy covariance measurements of CO₂ fluxes, combined with modeling, have shown that drought can cause a net loss of CO₂ from grasslands that are a net sink for CO₂ during wet years (Hunt et al., 2004; Novick et al., 2004). On a global scale, SOC also tends to increase with increasing precipitation and decrease with increasing temperature (Jobbagy and Jackson, 2000).

Although mean annual temperature during our study differed from the long-term average by only 0.08°C (Table 6), temperatures tended to be higher than normal during the dormant season (October–March) which would have increased soil respiration (Gilmanov et al., 2004), while the dry summers inhibited photosynthetic inputs. Loss of SOC may also have partially resulted from short-term disequilibrium in the C-cycling process during conversion from cultivated soils to pasture (Ammann et al., 2004). Corre et al. (1999) found that conversion from well-established C₃ grass stands to C₄ grass resulted in a loss of SOC during the early years of C₄ grass establishment. As many as 16 to 18 yr were needed before total SOC under the C₄ grass approached that under the original C₃ pasture. A similar recovery period may be necessary before newly established pastures become net SOC sinks.

A survey of 37 pastures in the northeastern USA found that SOC percentage was positively, but weakly, associated with species richness (Tracy and Sanderson, 2000). Positive, negative, or no effect of plant species diversity on soil biological activity and litter decomposition has been reported in the literature (see citations in Sanderson et al., 2004). In this study, the most species-rich pasture had the greatest above- and belowground biomass, yet experienced the greatest decrease in SOC. It is possible that root turnover rate was reduced in the 11-species mixture, increasing root biomass and slowing the transfer of plant C into the SOC pool.

Averaged across the 3 yr that photosynthesis and root biomass were measured, forage yield was 35% greater and root biomass in September was 30% greater in the 11- vs. the 2-species mixture. At the same time, there was

Table 6. Monthly temperature and rainfall data on a farm in Berks County, PA.

Month	Temperature						Rainfall					
	1999	2000	2001	2002	mean	Long-term avg.	1999	2000	2001	2002	mean	Long-term avg.
	°C						mm					
Jan.	–	–2.3	–1.5	1.7	–0.7	–1.6	–	31	62	55	49	95
Feb.	–	0.1	0.8	2.4	1.1	–1.0	–	46	56	19	40	70
Mar.	–	7.5	2.7	4.9	5.1	4.9	–	167	108	118	131	91
Apr.	–	9.8	10.5	11.4	10.6	10.6	–	70	72	102	82	94
May	16.6	16.1	16.1	14.2	15.5	16.4	–	120	83	89	98	115
June	21.0	20.4	21.0	21.0	20.8	21.1	–	181	90	123	131	111
July	25.4	21.0	21.0	24.1	22.1	23.7	13	34	73	10	33	103
Aug.	22.3	21.1	23.7	24.0	22.9	22.7	73	71	56	67	67	92
Sept.	18.7	16.6	17.0	19.3	17.6	18.6	308	135	100	86	157	111
Oct.	10.5	12.5	12.1	–	12.3	12.2	66	49	20	–	45	83
Nov.	8.3	5.4	8.9	–	7.1	6.8	70	60	52	–	61	90
Dec.	2.0	–3.2	3.7	–	0.2	1.2	55	78	63	–	65	84

only a 16% difference in midday photosynthetic rate. Obviously, differences in midday net photosynthesis were not sufficient to account for the increased production that was observed with the 11-species mixture. Several reasons could account for the discrepancy between midday net photosynthesis and biomass production. First, measurements of net canopy photosynthesis include soil respiration, which could have been greater in the 11-species mixture, masking the actual increase in gross photosynthesis. This is consistent with the greater loss of SOC that was observed in the 11-species mixture. Second, drought-stressed plants often have similar photosynthetic rates to nonstressed plants early in the day, while afternoon rates are significantly reduced under drought (Baldocchi et al., 1983). It is possible that the deeper root distribution and greater access to water with the 11-species mixture reduced the level of stress and allowed that mixture to maintain afternoon photosynthesis at rates that were comparatively greater than the 16% improvement over the two-species mixture that was observed at midday. Finally, including more species in the mixture could have extended the growing season by including species that commence growth sooner in the spring or extend growth later into the fall. Extending the length of the growing season could increase total productivity without requiring any increase in the daily photosynthetic rate.

CONCLUSIONS

Our results suggest that planting a complex mixture of forages without regard to the identity of the species in the mixture may not be wise. Only about half of the species planted in the 11-species mixture persisted during the entire 6-yr experiment. Still, the 11-species mixture yielded more forage dry matter than the two-species mixture, although this difference was probably due to the inclusion of a few highly productive forage species. The 11-species mixture also had increased photosynthetic rates during the summer, increased root production, and a greater depth of rooting. Contrary to our original hypothesis, this did not translate into a greater accumulation of SOC. Greater root biomass combined with deeper penetration into the soil profile should improve forage production during periods of drought stress by improving access to water in deeper soil layers that would not otherwise be available. Selecting forage mixtures to include specific desirable traits, such as improved drought tolerance or greater rooting depth, would most likely result in improved pasture performance.

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